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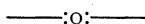
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ON THE NATURAL SUCCESSION OF THE DICOTYLEDONS.<sup>1</sup>

BY LESTER F. WARD, A.M.

THE system of classification for dicotyledonous plants now in use in most text books of botany is substantially that of Antoine Laurent de Jussieu, as published in his *Genera Plantarum* in 1789. Although many minor modifications have been made and are still being made by different authors, the fundamental arrangement into three "Divisions," depending on the nature of the corolla, has been maintained in its integrity to the present

<sup>1</sup> A sequel to the article on the *Genealogy of Plants* in the June number. The substance of the two articles was embodied in a paper read before the Philosophical Society of Washington, February 16, 1878.

day; only two serious attempts having yet been made to cut loose from it, one of which has failed to command an acceptance, notwithstanding the eminence of its author, while the other is still too new to permit an opinion as to its ultimate success. I refer to Dr. Lindley's classification as elaborated in his *Vegetable Kingdom*, and to the system proposed by Sachs in his *Text Book of Botany*.

In the first,<sup>1</sup> or, as it is supposed, highest of the three "Divisions," the corolla consists of distinct pieces or *petals* not at all connected with each other, and this is called the Polypetalous division. In the second group these petals are united, at least at their base, the distinct divisions only appearing, if at all, in the form of a "limb" of separate lobes at the summit of a tube of greater or less length. This group is called the Monopetalous division. The third group wants the petals and corolla entirely, the perianth consisting of a single envelope which is always assumed to be the outer or calyx. Plants of this nature form the Apetalous division; they are also frequently denominated monochlamydous, those of the other two divisions being designated as dichlamydous.

The defects of this classification have long been apparent, and although so persistently adhered to, it has always been a source of trouble to systematists, no two ever entirely agreeing as to its precise limits. Even those who wholly ignore or reject the doctrine of descent seek to bring together as nearly as possible those plants which actually resemble each other most, since this is the fundamental idea, and formerly the only idea, of a "natural system." Yet in adhering to the principle involved in the classification by divisions this was frequently impossible, the two principles being often in direct conflict. In every such case it is clear that the maintenance of the divisions involved, is so far, an *artificial*, as contradistinguished from a *natural* system of classification. And indeed it is difficult to see how a system of classification based on the corolla is more natural or less artificial than one based on the stamens. If it could be shown that this class of characters are

<sup>1</sup> The propriety of commencing text books of Botany or Natural History with the highest or most perfectly organized families and descending the scale so as to end with the lowest or most imperfectly organized may well be questioned. Though doubtless more convenient for beginners to study, it tends to antagonize and keep out of view the truth of a progressive historical development in living things which, to the majority of students, is of greater value than any technical acquaintance with specialized forms.

more permanent or reliable, or that they are more comprehensive, and better typify the general sum of the characters distinguishing groups of plants, a point in their favor would be gained, but, as we shall see, such is not the case. In point of fact these characters frequently change when nothing else has changed, and often remain the same when everything else widely differs. They constantly tend to "run together," and no strict dividing line exists between them. They also frequently vary within very narrow groups, sometimes in the same species or individual. Critically viewed, therefore, this system so far as it goes, presents as many imperfections and stands as directly in the way of the adoption of a truly natural system as did the professedly artificial one of Linnæus.

The recognition of the three Divisions, as is made in nearly all systematic works on botany, even the most recent, involves numerous direct conflicts with the best established orders of dicotyledonous plants. Many orders are found to contain species and genera whose corollas would require them to be placed in a different Division from that in which the order itself has been placed. Examples of this class are abundant. *Paronychia*, a genus which seems clearly to belong to the polypetalous order *Caryophyllaceæ* (*Illecebreæ*), is usually apetalous, though some species retain a rudiment<sup>1</sup> of the petals in the form of minute teeth or bristles; *Chrysosplenium* in the order *Saxafragaceæ* is another example of the same class. *Glaux* in the monopetalous order *Primulaceæ* is destitute of a corolla. *Ludwigia*, *Ammannia*, *Penthorum*, *Nyssa*, are further illustrations, and only the most familiar need be mentioned. Most of the *Euphorbiaceæ* in this country (if we except *Euphorbia* itself), which are monœcious, have polypetalous staminate (male), and apetalous fertile (female) flowers. Here we have the two extreme divisions united in the same individual plant (*Croton*, *Tragia*, etc.).

<sup>1</sup> The term "vestige" would probably be more correct. It is certainly remarkable that this term has not been more generally adopted to express this important distinction so clearly perceived by the naturalists of this epoch. The terms "rudiment" and "rudimentary" should be confined to those organs which the life-history of the plant or animal shows to be in process of development or formation. On the other hand those organs which, from disuse or other causes, have dwindled into mere remnants of once perfect ones should be distinguished by the term "vestiges" or an equally appropriate and expressive one. Yet these are the so-called "rudimentary organs" which have played so great a rôle in the modern theories of science, and Mr. Darwin himself employs this expression in that sense without commenting on its bad etymology.

Again, there are cases in which the lobes of the nominally gamopetalous corolla are so deeply parted that it becomes difficult to determine whether they are at all united, and in which the union sometimes actually ceases to exist. Of this class might be mentioned at random *Symplocos*, *Statice*, *Naumbergia*, *Anagallis*, *Chionanthus*, *Fraxinus*. The last named genus is of special interest in consequence of the close general resemblance between the ash and maple families, which are, however, widely separated in the present system. That beautiful climber, *Boussingaultia baselloides*, commonly known as the Madeira vine, is botanically related to the *Portulacaceæ*, but the petals are barely united at the base, for which reason it has been removed from its natural association and placed in the monopetalous division.

Thus we find that while some botanists have preferred to maintain well established orders intact by allowing them to embrace genera and species whose corolla would require them to be placed in different divisions, others have chosen rather to remove such anomalous genera to their appropriate divisions and if necessary to create new orders for them. Some, for example, leave *Paronychia*, *Anychia*, etc., in the *Caryophyllaceæ*, with which they are clearly allied, while others place them in the apetalous division near the *Polygonaceæ* with which they doubtless are also allied. But there are many cases which cannot be thus easily disposed of, as the *Aquifoliaceæ*, *Euphorbiaceæ*, *Asclepiadaceæ*, etc., in which cases the entire order is changed about from one division to another, according as the author may think the preponderance of characters requires.

Not only does it frequently occur that an order which cannot be divided contains genera representing two of the general types of corolla upon which the divisions are founded, but some orders, as the *Primulaceæ*, actually embrace all three of these types. In the order just named we find *Naumbergia* which is frequently polypetalous, and *Glaux* which is always apetalous, while most of the genera are monopetalous.

These few examples, which might easily be extended, certainly show that the so-called divisions of the *Dicotylæ* do not form a natural series. They rather indicate that they represent three parallel and co-ordinate series, in any one of which orders closely corresponding may be named in one or both the others. Thus the *Caryophyllaceæ* may be compared with the *Polygonaceæ*, the *Acer-*

*inæ* with the *Oleaceæ*, the *Aquifoliaceæ* with the *Rhamnaceæ*, the *Malvaceæ* with the *Euphorbiaceæ*, and the *Hamamelaceæ* with the *Platanaceæ*. These comparisons and others that will suggest themselves to every botanist, reveal natural relationships between plants which are far removed from each other because they fail to agree in the one character on which the divisions are based. They clearly show, therefore, that the arrangement by divisions is an artificial one, and that the fact of the coherence or non-coherence of the petals is far from a reliable one as indicating the true succession, much less the genealogical descent of the families.

It is not claimed, however, that the three mostly parallel series wholly fail to express any general law of the vegetable kingdom, and an attempt will be made before concluding the subject to show that they do express in a partial manner an important truth in phytonomy. Though concurrent for a great part of their length and inosculating all along, these lines of development appear not to have had a simultaneous origin. But before entering upon the direct treatment of this problem it will be necessary to consider another class of facts.

The practice thus far dwelt upon of distorting the natural system by an undue regard for the corolla is only one example under a general class. The vice itself expressed in general terms, is that of adhering too closely to any one character to the neglect of all the rest. We thus find cases within the same division in which orders unquestionably allied are not placed together, but are widely separated. Every one has been struck by the resemblance of certain Ranunculaceous with certain Rosaceous plants, especially as to foliage and general habit; for example, *Ranunculus* with *Geum*, *Actæa* with *Spiræa*, etc. It is customary with botanists to affect a certain degree of contempt for such general resemblances, and they are commonly regarded as wholly misleading. That they cannot be depended upon as safe guides to special investigation all will of course admit, since it so frequently happens that striking similarities exist between families which cannot in any way be assimilated. But even in such cases the resemblances often vanish on closer inspection and prove to have been produced by entirely dissimilar processes. General resemblances which will bear close inspection are rarely without a meaning. There is a certain correlation which subsists

among all the characters of a plant so that those which have similar organs of reproduction usually exhibit strong family relationships. Were it not so familiar it would be a surprising fact that a Solanaceous plant can usually be detected as such without examining the flowers, merely by a certain undefinable appearance which belongs to the family. The same is true to a greater or less extent with all the large orders, *Cruciferae*, *Borraginaceae*, *Urticaceae*, etc. In some families still more subtle characteristics persist with great uniformity, of which the peculiar odor of the *Orchidaceae* is a good example.

This so-called "general aspect" is in reality the *ensemble* of all the characters which make a plant such as it is, and though any one character is as liable to vary as another or as more obvious ones, their number is so great that it requires an enormous period of time to so efface them all as to destroy all traces of resemblance. Not so of any particular character which botanists may fix upon. This may vary in a manner comparatively rapid, and thus it doubtless often happens that species really related and bearing a general resemblance are divorced in the text books on special differences.

This co-existence of so large a number of minor peculiarities as to give to two plants or groups of plants an obvious general resemblance should therefore be welcomed as a valuable accessory to the work of classification, not as a special guide to truth but as a general check upon error. A strong *physiognomic* resemblance between two groups of plants should at least raise a suspicion of their genetic relationship, and might frequently furnish a theory for the investigation of important questions. In a previous paper it was shown how the physiognomy of the *Cycadaceae* pointed to their natural position between the ferns and the palms, and how a closer inspection of the more reliable characters sustained this conclusion. If now we return to the case of the *Ranunculaceae* and *Rosaceae* above referred to, we shall find a further confirmation of this law. A careful comparison of all the genera of these two orders, which has been recently made, reveals the fact that there is to be traced "an easy transition from the wholly conical and much elongated receptacle of *Ranunculus* and *Myosurus* to that of *Fragaria*, flattened at the base and conical in the center, or of *Rubus* with its raised margin and convex center. From this we may pass to *Sibbaldia*, *Potentilla*, *Horkelia* and

*Stylobasium*.”<sup>1</sup> On the same principle the *Portulacaceæ* have been very closely assimilated to the *Cactaceæ*, with which they are found to agree in an astonishingly large number of characters, including that of the irritability of the stamens. Again the *Droseraceæ* and *Saxifrageæ* are now known to be closely allied families, as their physiognomy would indicate. And strange as it may at first appear, there is little doubt that the *Cruciferaæ* are related to the *Onagraceæ* by natural affinities more or less close. Further investigations from the same point of view will doubtless enable us to go much farther in discovering the true affinities of dicotyledonous plants.

It is undoubtedly the special function of the floral envelopes, as it is of the ovary, to protect the germ, and the degree of this protection is the most reliable index we have to the degree of advancement in vegetal life. The means employed in securing this end in the *Dicotylæ* are two-fold: first, the relation in which the calyx stands to the ovary; and second, the character of the inner envelope or corolla. Botanists, while they have not ignored either of these essential characteristics, have generally placed more weight upon the second than upon the first, although for the purpose named the first has doubtless been of equal service to plants.

From the hypogynous to the perigynous, and from this to the epigynous calyx-tube, there is certainly a steady progress in the direction of protection, and the advance of the calyx towards the more complete enveloping of the ovary may be regarded as indicating an equivalent advance in organization. In Dr. Lindley's great work on *The Vegetable Kingdom*, this was made the leading character, although in his earlier works he had followed the system of Laurent Jussieu; and Prof. Julius Sachs in his *Text Book of Botany*, though in most respects making an entirely new departure in botanical classification, places the *Rosaceæ*, *Onagraceæ*, *Myrtaceæ*, and other strictly epigynous families at the head of the system as representing the highest type of development.

The classification by divisions, on the other hand, professes to give special prominence to the corolla as an index of progress, but how obscure the notion of any direct advantage to be derived from it to the plant must have been with the founders of that sys-

<sup>1</sup> Baillon, *Histoire des Plantes*.



tem, is shown by the order in which the divisions were arranged. It seemed evident to their minds that those plants which were wholly destitute of a corolla, the apetalous or monochlamydous division, should stand at the base, and thus far they were certainly consistent. But in placing the polypetalous division at the head of the system, the idea of its protecting function must have been quite forgotten. For unquestionably the monopetalous corolla is the form of floral envelope which affords the greatest protection to the ovary and stamens, and the more nearly this approaches to the tubular form the more complete is that protection. The distinct, usually spreading, and often fugacious petals of polypetalous plants are of very little service in this respect, so that, in so far at least as this one principle is concerned, they should certainly stand next above the *Apetalæ*.

In this respect too, it is true, certain monocotyledonous plants would take a higher rank than some apetalous and polypetalous *Dicotylæ*, their tubular perianths forming better protecting envelopes. But as it is the genealogical series that the new taxonomy seeks, other more fundamental characteristics must preclude all attempts to derive the *Monocotylæ* from any advanced stage of the *Dicotylæ*.

The general truth, which is becoming more and more apparent, is that the floral envelopes cannot alone be relied upon to indicate the course of development of the Dicotyledons, and that for the natural arrangement of the families many other considerations must be taken into the account. Instead of depending upon any one character it is necessary to consider all the characters together. The task, it is true, is vastly more difficult, and systematic botany becomes a science requiring exhaustive study, but the conclusions reached will be correspondingly more valuable.

One of the best checks by which the genealogical systematist may frequently orient himself, is what has been called the "physiognomy" of plants. Whenever the pursuit of any particular character or set of characters is found to have brought into close proximity plants of a totally different physiognomy, it is generally safe to conclude that the process has been carried too far; and on the other hand, when, as is frequently the case in the present system, plants having strong general resemblances have been widely separated, the propriety of reviewing the evidence

on which such separation was based is at least strongly suggested. The resemblance, above pointed out, which the *Caryophyllaceæ* bear to the *Polygonaceæ* illustrates this. In these orders the corolla and the ovary, two of the most reliable characters, are sufficiently distinct in typical genera to justify a separation, but when led by the stipules, swollen joints, leaves, habit, and other peculiarities that combine to make up their general appearance, to place them in juxtaposition and study them comparatively, we find that even these characters fail in certain genera, while the relationship indicated by the physiognomy is partially supported by more respectable evidence. We have already seen that several members of the chickweed family are apetalous. On the other hand some genera of the *Polygonaceæ* may be regarded as at least functionally dichlamydous, as in *Chorizanthe*, the one-flowered involucre closely imitating a calyx. And further, the capsule of several genera of the *Caryophyllaceæ* (*Paronychia*, *Anychia*, *Scleranthus*) is reduced to a one-seeded utricle approaching the achenium of the buckwheat family.

While, therefore, the time has not yet arrived for the attempt to be made to trace out the line of genealogical descent of the Dicotyledons, it is evident that a complete re-adjustment of the orders, to a great extent independently of the present divisions, will have to be made and might soon be undertaken.

The first dicotyledonous plants were in all probability apetalous, and all authors agree in placing the *Amentaceæ* (*Fuliflores* of Sachs) at the bottom of the scale. It is certainly not without significance that the *Casuarineæ*, whose possible descent from the *Guetaceæ* (*Ephedra*) was referred to in the previous article, belong to this group.

The origination and development of the corolla was doubtless by a process similar to that by which the calyx was formed. In both cases it was the advantage, however slight, which the plant derived from it that occasioned its progressive development into a protecting organ. In the *Amentaceæ*, as also in many *Monocotylæ* (*Cyperaceæ*, *Gramineæ*), these envelopes are very imperfect, often reduced to mere scales. Polypetalous plants (and doubtless apetalous also) may be of two kinds, according as the petals may be shown to represent rudiments of a gamopetalous corolla in process of development, or only *vestiges* of one which they formerly possessed. The terms "polypetalous" and "monopet-

alous" do not properly designate the process by which these organs are developed. According to the accepted principles of phyllotaxy, each petal (as also each sepal) represents a transformed leaf; but the embryological study of those plants in which the corolla takes the form of a tube, has proved that this has not been produced by the union of the original petals, but by the formation at first of a ring at their base which acquires greater prominence until it eventually assumes the character of a tube. To better indicate this process the terms "eleutheropetalous" and "dialypetalous" are employed by certain authors to denote that the petals are distinct, the term "gamopetalous" being used for the very objectional one "monopetalous."

If natural selection has had anything to do with the development of these organs, it is certain that the free petals must have historically preceded the tube, and hence we may conclude that for the earliest forms of each division the order of succession was: first, *Apetalæ*; second, *Eleutheropetalæ*, and third, *Gamopetalæ*, and therefore to whatever extent these divisions may now be parallel and coördinate, they were not so at the outset.

If, therefore, we were to accord to the general principle of protection, as above pointed out, its full force in the classification of dicotyledonous plants, at the same time keeping in view certain subordinate laws by which it is qualified, we should probably find, in attempting to reconstruct the present system, that while the so-called divisions would be virtually abolished and the orders within each very much blended and intermixed with those of the others, there would still remain an ascending series based on the perfection of the floral envelopes, and in which as now those plants classed as apetalous would in the main stand at the base. The intermediate terms of this series would, however, unlike the present system, consist chiefly of those orders now placed in the polypetalous division, while the highest of these terms would be represented by the monopetalous orders with tubular corollas. This arrangement would be further modified by the relation of the calyx to the ovary and minor considerations. In fact, if the true genealogy of the *Dicotylæ* is ever worked out it will doubtless be found to conform to the general law in all departments of life, and to assume the arborescent form, whose ultimate ramifications it would be wholly impossible to trace in the present state of the science.

Very little more than this can at present be predicted with regard to what the true "Natural System" really is, which we are still so far from understanding; but it would seem from the peculiar character of *Compositæ*, and especially from the double safeguard of their narrowly tubular corollas, their epigynous calyx (*pappus*), and syngenesious anthers, still further secured by the massing of the flowers into dense heads, that this order, which is also the largest in the vegetable kingdom, should be regarded as the highest and most specialized family of plants, and might be fitly made to crown the natural system.

The general arrangement above outlined is further substantiated by the limited data which palæontology affords. The greater part of the fossil plants of this class have been found in the Cretaceous formation. They nearly all belong to the apetalous and polypetalous Divisions, but by far the greater number to the former; such genera as *Salix*, *Quercus*, *Platanus*, *Sassafras*, etc., occur most frequently, and some of these have been traced to the lowest Cretaceous strata if not to the Jura. That they existed in still earlier times can scarcely be doubted, and high authorities have fixed upon the Trias as the probable epoch in which the earliest dicotyledonous genera made their appearance. In the Upper Cretaceous certain polypetalous genera begin to be found, among which are numbered *Magnolia*, *Liriodendron*, *Prunus* and other multi-staminate plants, most of which have been assigned a high rank in the current system. This fact and others seem rather to indicate that a great many stamens and an elongated receptacle are marks of a low organization, as if just emerging from the catkin-stage. Very few gamopetalous plants are found fossil, strongly implying that they belong to late Tertiary periods. Especially significant is the absence of those having elongated tubular corollas, while it is believed that the first fossil *Composite* plant is yet to be discovered.

Little, therefore, as is really known of the natural succession and actual genealogy of the Dicotyledons, we may, nevertheless, fairly claim to have acquired sufficient data to warrant entering upon the investigation of this difficult and complicated problem, a task which must owe a great share of its success to the aid to be rendered by a rational hypothesis.